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Lake Trout Movements in U.S. Waters of Lake Huron Interpreted from Coded Wire Tag Recoveries in Recreational Fisheries

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ABSTRACT. *Lake trout management and restoration make use of age-structured population models that incorporate parameters to represent movement among management areas, and harvest quotas are based on proportions of stocked fish remaining in and moving out of areas of release. We investigated movements of lake trout in U.S. waters of Lake Huron based on spatial and temporal distributions of coded-wire-tag (CWT) recoveries by trip in recreational fisheries using Generalized Linear Models (GLMs). For the analysis, we incorporated as model predictors the area, month, year, and source of CWT recovery, which included reports by charterboat captains, creel-clerk interviews of non-charter anglers, and "headhunter" (CWT collection specialist) samples from charter and non-charter catch. Results indicated that CWT recoveries by trip were lowest from charterboat operators, followed by recoveries from creel clerks (2× captain reports), headhunter non-charter (3×), and headhunter charter (9×). Standardized recovery levels were highest in the management area of release and one area immediately adjacent, with remaining percentages decreasing with distance from release. CWT recovery levels decreased from May to September and suggest seasonal movement among areas that have implications for stock assessment. From standardized recoveries, we estimated that 40% of the CWT lake trout were recaptured in areas where released and others moved north, south, and southeast. Our results indicate that higher proportions of lake trout move out of release areas fish than previously shown and suggest that prior studies may be biased, in part due to lack of standardization among tag recovery sources and ignoring seasonal movements.*

INDEX WORDS: *Lake trout movement, Lake Huron, tags, Generalized Linear Models.*

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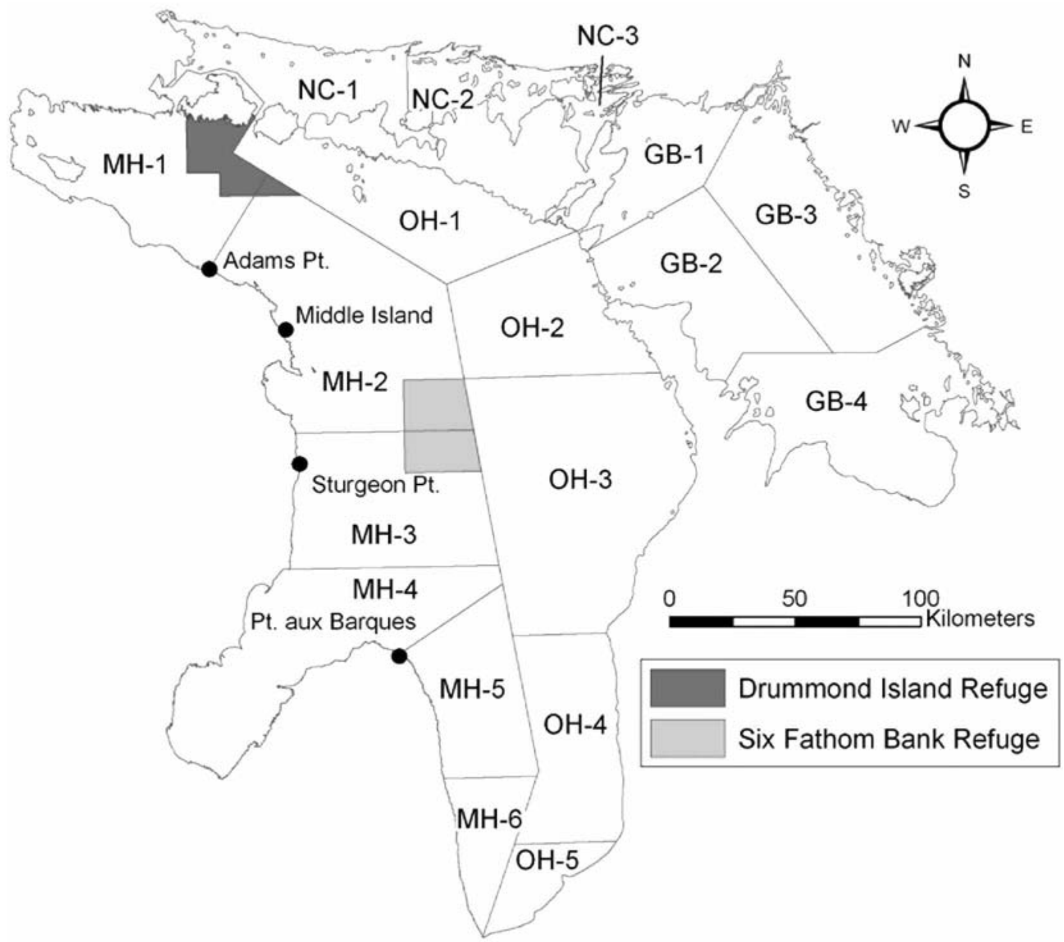

FIG. 1. Statistical districts of Lake Huron (US: MH-1 to -MH-6; Canada: OH-1 to OH-5, NC-1 to NC-3, and GB1-GB-4). Solid circles indicate sites where tagged lake trout were released in stocking areas along the coast. Tagged fish were also released in locations within refuges.

INTRODUCTION

Collapse of lake trout (*Salvelinus namaycush)* stocks in the Great Lakes, and consequent rehabilitation efforts, have been well documented (i.e., Hile 1949, Eschmeyer 1957, Lawrie 1970, Coble *et al.* 1990, Eshenroder *et al.* 1995). In Lake Huron, lake trout stocks collapsed in the 1940s, and stocking of hatchery-raised fish began in 1973. Since the early 1980s, spawning populations have been re-established in some areas but their contribution to the lake trout population of Lake Huron's main basin is insignificant (Johnson and VanAmberg 1995). Efforts to rehabilitate self-sustaining populations through stocking and harvest management are ongoing (Eshenroder *et al.* 1995, Johnson *et. al.* 2004).

In Lake Huron, lake trout stocking experiments employing coded-wire-tags (CWT) were initiated during fall of 1985 in the Drummond Island and Six Fathom Bank refuges (Fig. 1) to examine performance among lake trout strains. In 1992, a strain controlled movement study was initiated at nearshore sites to study movement patterns, growth, survival, and reproductive success. About 1 to 2 million lake trout, 20% marked with CWTs (Table 1), have been stocked annually in U.S. waters. In Canadian waters, less than 1 million lake trout have been stocked annually, approximately 2% marked with CWT.

Lake trout stock assessments make use of age-structured population models (Johnson *et al.* 1995, Sitar *et al.* 1999, Woldt 2003, Johnson *et al.* 2004, Woldt et al. 2005, Woldt et al. 2006) that require inclusion of parameters to represent movement

TABLE 1. Number of lake trout marked with CWT tags and stocked in Michigan statistical districts of Lake Huron (Fig. 1) from 1985 to 2000 (from Fish Stocking Database, Great Lakes Fisheries Commission, www.glfc.org).

	Statistical Districts				
Year	MH-1	MH-2	MH-3	MH-4	Total
1985	104,094	—	271,268	—	375,362
1986	—	—	—	—	—
1987	187,566	—	230,800	—	418,366
1988	—	—	221,300	—	221,300
1989	147,000	—	202,100	—	349,100
1990	138,700	—	194,300	—	333,000
1991	127,000	—	184,900	—	311,900
1992	191,800	60,000	253,000	58,500	563,300
1993	130,200	190,800	—	—	321,000
1994	59,400	182,200	60,000	62,100	363,700
1995	128,680	184,900	—	—	313,580
1996	190,900	229,850	56,100	59,900	536,750
1997	135,300	177,100	—	—	312,400
1998	181,200	231,900	54,200	56,200	523,500
1999	118,700	—	—	—	118,700
2000	117,396	—	192,280	—	309,676
TOTAL	1,957,936	1,256,750	1,920,248	236,700	5,371,634

among management areas, usually in the form of transition matrices. To develop such matrices for lake trout movement in Lake Huron, Woldt (2003) and Madenjian et al. (2003) used recoveries of CWT fish (Table 2). Woldt (2003) implemented a transition matrix to allocate lake trout in areas of the 1836 treaty-ceded waters of Lake Huron and stocked at inshore locations and in lake trout refuges (Fig. 1). The matrix is used for management and adjusts the numbers of lake trout for movement soon after stocking (before spatially-varying mortality occurs), by assigning fixed proportions as being effectively stocked into U.S. management areas where they moved. The reason for adjusting immediately after stocking is the unavailability of age 1 returns. Matrix cells were calculated as the proportions of the total CWT recoveries expressed as catch per 305 m of gillnet per 100,000 CWT lake trout stocked from one area that were recovered in each management area based on returns through 1999. Data to implement the matrix were recoveries from agency surveys conducted lake wide using graded mesh (5.1 to 15.2 cm) and large mesh (> 11.4 cm) gillnets and from commercial fishery

TABLE 2. Percentage of lake trout recovered by statistical districts in Lake Huron (Fig. 1) given the district of release from Madenjian* et al. *(2003) and Woldt (2003). In Woldt (2003), MH-3 includes all areas south of MH-2. DI = Drummond Island, SF = Six Fathom Bank.

	Release Areas									
Recovery	Madenjian et al. (2003)				Woldt (2003)					
Areas	MH-1	MH-2	MH-3	MH-4	MH-1	DI	MH2	MH-3	SF	MH-4
MH-1	64.2	33.2	4.8	0.4	71.9	97.3	34.9	9.7	4.83	0
MH-2	24.0	41.8	26.0	3.2	22.9	1.3	54.8	35.5	9.1	13.2
MH-3	5.8	14.0	34.5	9.2	5.1	1.3	10.3	54.8	86.1	86.8
MH-4	1.3	2.8	9.3	26.2						
MH-5	1.1	1.3	7.1	21.1						
MH-6	0.1	0.1	0.5	2.0						
NC 1-3	0.2	0.2	0	0.1						
OH 1-5	3.3	6.6	17.8	37.8						
GB-2	1	0	0	0.1						

catches. Data between gear types were standardized according to Gulland (1969). Data from recreational fisheries were excluded because of problems with standardizing recovery effort and efficiency among recovery sources. Madenjian *et al.* (2003) calculated a similar proportion matrix using recovery data from CWT fish released in inshore stocking locations and recovered from surveys, commercial catch including small and large mesh gillnets as well as trap nets, and partially from recreational fisheries in all Lake Huron management areas from U.S. and Canadian waters. Calculations were not adjusted for differences in effort or efficiency among recovery sources. The need to standardize CWT recoveries for recovery sources, particularly from recreational fisheries, remains an issue.

Previous studies describe lake trout movement in the Great Lakes as localized, although some individuals may travel distances over 400 km (Smith and Van Oosten 1939, Eschemeyer *et al.* 1953, Buettner 1961, Rahrer 1968, Pycha *et al.* 1965, Swanson 1973, Rybicki and Keller 1978, Hansen *et al.* 1995, Schmalz *et al.* 2002), with the extent of movement increasing with fish age, size, or density (Schmalz *et al.* 2002). For example, in western Lake Michigan, Smith and Van Oosten (1939) reported that 77% of tagged trout were caught within 80 km of a tagging location. Schmalz *et al.* (2002) found that 90% of lake trout tagged in Clay Banks, northwestern Lake Michigan, remained within 68 km of the stocking location regardless of tagging year or recapture season. Rybicki (1990) found that almost all lake trout stocked as yearlings in the Lake Michigan Northern Refuge were recaptured as yearlings in the vicinity where they were stocked; but by age 2 some lake trout had dispersed as far as 120 km, and by ages 3 and 4 some had traveled to southern Lake Michigan, a distance of more than 400 km. In Lake Huron, studies also show that, although movement is mostly localized, some marked individuals can be found as far as 300 km from their release areas (Ebener 1998, Madenjian *et al.* 2003). Ebener (1998) reported that fish stocked at Six Fathom Bank (Fig. 1) were recaptured throughout the main basin, but most of those recoveries (56%) occurred within the Six Fathom Bank reefs. Madenjian *et al.* (2003) reported that in fall surveys nearly 50% of the tagged fish released in offshore refuge areas were recaptured within the stocking locations, while more variable spatial distributions were reported for CWT fish stocked at inshore release areas (20 to 60% at stocking sites, with levels decreasing toward the south, Table 2). Although lake trout movement patterns in Lake Huron have been described, the studies were not based on standardized CWT recoveries from all sources including recreational fisheries and are potentially biased. Therefore, further analysis of tagging data is required.

Tag recovery data are useful for investigating fish distributions relative to stocking sites and inferring movement patterns, but it is necessary to weight recoveries for the effort spent catching fish and recovering tags (Hilborn 1990, Schmalz *et al.* 2002), and also for the efficiency in collecting tags from different recovery sources. In Lake Huron, tagged fish are caught by commercial or assessment operations using gillnets, and by recreational fisheries using hook and line, for which the units of effort respectively correspond to a gillnet set per night and a fishing trip (or number of fishermen per hour fishing). Because adjustments can be made only for sources of recovery with equivalent units of effort, these CWT recovery data cannot be combined in a common analysis. In this study, we used data from the recreational fisheries that had been disregarded or partially incorporated in previous studies without standardization. These data provide spatial and temporal coverage that permit analysis of movement direction and seasonality, but exclude refuges where only assessment surveys have access. In Lake Huron recreational fisheries, lake trout are caught by charter and non-charterboat anglers, and CWT fish are recovered by several sources. We standardized CWT recovery data from recreational fisheries for effort and efficiency among recovery sources, and investigated spatial and temporal distributions of CWT fish to infer movement.

MATERIALS AND METHODS

Data Sources

We evaluated CWT recoveries and fishery data from Michigan waters of Lake Huron from four independent databases including the Michigan Department of Natural Resources Coded-Wire-Tag (MDNR CWT) database, and the MDNR Creel, Charterboat and Headhunter Fishery databases. We did not include data from the Canadian recreational fisheries in our analysis because CWT recoveries were extremely scarce, CWT recovery and fishery data were not available at the level of detail required for this study, and also because of differences between fishery monitoring surveys and tag recovery programs. For example, a Headhunter

(CWT collection specialist) program only exists in the U.S.

The MDNR CWT database is the most comprehensive database available of CWT recovered from recreational fisheries in the upper Great Lakes, and contains information on individual tag recoveries. CWT fish in U.S. waters are marked at U.S. Fish and Wildlife Service hatcheries as fingerlings or yearlings with a small piece of wire with an engraved code into the fish's snout as described in the MDNR web page (www.michigan.gov/dnr/z0,1607, 7-153-10364_10951_11301-97831—,00.html). Adipose fins are removed to aid quick identification of recovered marked fish by external examination. Following tagging and mark quality control testing, the fish are released at stocking sites. When fish with missing adipose fins are recovered, the snout is removed for processing. Tags are detected with a "V-box detector" or a hand-held wand detector. The sample is serially bisected and scanned until the tag is visible to the unaided eye and can be removed using a magnetized "pen" or knife. The "code" is read under a microscope and data are entered into the CWT database. CWT recovery programs, and processing of tags, are carried out through collaborative efforts of the U.S. Geological Survey-Great Lakes Science Center (GLSC), Michigan Department of Natural Resources (MDNR), Chippewa-Ottawa Resource Authority (CORA), Ontario Ministry of Natural Resources (OMNR), U.S. Fish and Wildlife Service (USFWS), and various fishing groups. In the recreational fisheries, marked fish are recovered from the chartered and non-chartered fisheries through creel census and headhunter programs during interviews that take place on shore at the completion of fishing trips. CWTs also are recovered by charterboat captains who are required to report catches but not to return CWT fish, and anglers that voluntarily sample tags.

We analyzed 1,566 records of CWT fish recovered in Lake Huron recreational fisheries from 1993, when the headhunter program started, to 2000. We didn't include 958 records voluntarily reported by anglers because recovery effort was unknown, and 20 records from fishing tournaments because recovery effort was significantly different than normal. We selected CWT data from fish recovered from May through August and during a few days in September. Most records were from tagged fish released in stocking locations in north-central Lake Huron within U.S. management areas defined as statistical districts MH-1 to MH-4 (Fig.1). About 80% of total records were from releases in offshore areas (Six Fathom Bank and Drummond Island Refuge), and the rest were from releases in inshore areas along the lake western coast (Adams Point, Middle Island, Sturgeon Point, and Point aux Barques) (Fig.1). Most CWT recoveries were from the non-charter fishery (1,334) and were sampled in equal numbers by creel clerks and headhunters (Table 3). The highest numbers of tagged fish were recovered in statistical district MH-2 (543 in MH-2, 476 in MH-3, 267 in MH-5, 138 in MH-4, 127 in MH-1, and 15 in MH-6).

The MDNR Creel Database provided information by fishing trip from recreational fisheries on date and site of the interview, fishing site and mode, time starting and ending the fishing operation, number of anglers by trip, target species, and catch information by species. Information in charterboat and headhunter files was similar to that in creel files except that target species were not reported. To pair CWT recoveries with the trips where tags were recovered, we aggregated both the CWT and the trip data by month and statistical district of recovery (Fig. 1), and matched the number of CWT fish and the corresponding effort for each source of recovery.

Estimation of Fishing Effort to Recover Lake Trout Marked with CWTs

We used the trip as a measure of fishing effort and estimated effective effort by excluding trips with very low chances of catching lake trout. Recreational fisheries in Lake Huron target multiple species. The main potential source of bias for this

TABLE 3. Number of lake trout marked with CWT recovered in the non-chartered fishery by creel clerks (CCK) and headhunters (HHR), and in the chartered fishery by headhunters (HHB), and reported by captains (CBT).

Year of recovery	Source of recovery				
	CBT	CCK	HHB	HHR	TOTAL
1993	6	5	0	11	22
1994	3	14	1	56	74
1995	14	114	5	85	218
1996	45	132	9	86	272
1997	32	93	10	97	232
1998	33	109	18	93	253
1999	25	126	34	164	349
2000	0	93	0	53	146
TOTAL	158	686	77	645	1,566

study is that targeting some species could result in trips with zero probability of catching lake trout; the variation in the proportion of such trips in time and space would cause fluctuations in average recoveries by trip unrelated to CWT fish numbers. Therefore, we identified those trips and excluded them from the analysis. We used the declared target species and the catch composition by target. We found that in the catch from the non-charter fishery, lake trout were absent in trips declaring 14 out of the 25 established target species and were present in trips targeting lake trout, brown trout (*Salmo trutta)*, Chinook salmon (*Oncorhynchus tshawytscha)*, rainbow trout (*Oncorhynchus mykiss)*, salmon and trout, trout salmonines, and walleye (*Stizostedion vitreum)*. Thus, we estimated effort excluding trips from all other targets, and also excluded trips targeting walleye since only 21 lake trout were caught in more than 11,000 trips. In the catch from the charter fishery, we found that lake trout for the most part were absent when yellow perch were caught, and we excluded those trips from our calculations. We included trips for which no fish of any species was caught, as the probability of having targeted lake trout could not be ruled out. These trips represented less than 5% of the 24,550 trips in the databases and the inclusion criterion should be of minor importance. Based on these criteria the number of trips selected as fishing effort for lake trout from both fisheries ranged from around 9,000 to 12,000 per year, and was highest in statistical district MH-1 to MH-3.

Spatial and Temporal Distribution of CWT Recoveries from Different Sources

We incorporated the type of fishery and the recovery program in our analysis to take into account differences in efficiency among recovery sources. In general, charter fishing trips have higher catches per trip than the non-charter fishery because the number of anglers per boat is, on average, double that in non-charter operations, trips tend to be longer, number of rods per angler is higher (although not reported), and captains have greater experience in catching fish. Efficiency in recovering CWT fish varies among programs because headhunters specifically sample fish heads, creel clerks do not sample CWT tags or heads in every interview, and captains are not required to report CWT fish.

We used a regression approach to investigate the temporal distribution of CWT-marked fish and modeled recoveries caught by trip, and index of relative abundance, as a function of variables representing spatial and seasonal distribution and the source of recovery (fishery/recovery program). We accounted for annual variation in CWT releases and mortality by introducing year as a factor in the models. Ideally we would incorporate the target species as a variable in our analysis, but this information is only available from the non-charter fishery. We did not consider lake trout age in our analysis because sample sizes were too small, and 70% of the fish were 4 or 5 years old. Further, CWT recoveries were too scarce to separately consider analysis of recoveries of CWT fish released in inshore and offshore locations. Skill variation among anglers was not considered as the angler identity is confidential, and information that allows identifying individual anglers is not recorded. We used Generalized Linear Models GLMs (McCullagh and Nelder 1989), the most appropriate approach for standardizing catch and effort data (Hilborn and Walters 1992, Goñi *et al.* 1999, Maunder and Punt 2004). We used the following model:

$$g(\mu_{ymdg}) + \alpha + \delta_y + \phi_m + \lambda_d + \tau_g \qquad (1)$$

where g () is a link function, μ is the expected number of CWT lake trout recovered by the corresponding number of trips, δ is the year, ϕ is the month, λ the statistical district, and τ the source of tag recovery. All variables in the linear predictors were introduced as factors. We used a binomial probability to describe the chance of recovering a number of CWT fish given the number of trips. Each trip was treated as a Bernoulli trial with the expected catch of CWT fish constrained between 0 and 1. Although multiple CWT recoveries are possible, μ was always very small because fishing regulations established daily allowances of only 5 salmonids, including no more than 3 lake trout, the preferred species of salmonids was Chinook salmon, 20% of the lake trout were tagged, and the available number of legal-sized CWT lake trout was relatively low. Exploratory use of a Poisson distribution resulted in inappropriate model fit, as the recoveries were too scarce. To select the link function relating the response variable to the linear predictor, we compared model deviance using the link functions suitable for binomial models: logit or logistic (log (μ/(1 – μ))), complementary log-log (log (–log(1 – μ)), and probit or inverse Normal (qnorm(μ)) (McCullagh and Nelder 1989).

We performed analysis of deviance and tested if

TABLE 4. Analysis of deviance table for main effects of a binomial GLM fitted to CWT lake trout recoveries by fishing trips in Lake Huron recreational fisheries, and model coefficients for the source of recovery (reports by captains, samples by headhunter from charter trips, and samples by creel clerks and headhunters from non-chartered trips). Analysis of deviance was performed by comparing the full model with models excluding one predictor at a time. Df = degrees of freedom. Coefficient are in logit scale. Reporting by charterboat captains was used as reference and coefficients for other levels express the difference between other recovery sources and the reference level. Index corresponds to the transformed coefficients relative to the reference = 1.

Terms	Residual deviance	Df	Deviance	Pr of (Chi)
Null model	4,223.6			
Recovery source	2,438.3	3	477.4	< 0.00001
Month (05–09)	2,855.9	4	894.1	< 0.00001
Year (1993–2000)	2,245.6	7	284.6	< 0.00001
Area (MH-1–MH-6)	2,612.0	5	651.0	< 0.00001
Full model	1,960.6			
Coefficients	**Value**	**Standard error**	**t- value**	**Index**
Charter captains	–5.975	0.109	–54.879	1
Non-charter creel	0.611	0.092	6.662	2
Charter headhunter	2.601	0.150	17.327	9
Non-charter headhunter	1.422	0.090	15.686	3

variables were significant by comparing full models with models excluding the tested variables one at the time. Relevant first order interactions were tested (see below) while higher interactions were not considered because insufficient data were available for many variable combinations. All tests were performed at the 95% confidence level. We checked validity of model assumptions and evaluated model performance. We ran GLMs using routines contained in the S-Plus programming environment (Becker *et al.* 1988, Venables and Ripley 2000).

Steps in the GLM analysis

i) To investigate variation of recoveries by trip among recovery sources, we ran main effect models for all recovery data available (May to September 1993–2000) and tested first order interactions between source of recovery, and month, statistical districts and year. ii) To investigate fish distributions relative to their areas of release and seasonal movements among areas, we ran models for recoveries of fish released in each statistical district (defined in Fig. 1), and tested first order interactions between month and recovery area. We included months and years for which sufficient data were available (May to August, 1995 to 2000). When interactions were significant, indicating differences in seasonal patterns in recoveries, we selected the month with highest recovery levels and ran month specific GLMs to derive coefficients for the movement matrix. iii) To infer movement we constructed a movement matrix, similar to Woldt (2003) and Madenjian *et al.* (2003), by calculating the percentage of the standardized number of recoveries from releases in each statistical district that were recovered by statistical district relative to total recoveries. Also, we calculated percentages based on non-standardized recoveries to investigate the effect of ignoring differences in effort and efficiency by recovery source.

RESULTS

Comparison of Efficiency among Recovery Sources

CWT recoveries by trip varied significantly among recovery sources (Table 4), with highest overall estimated levels when headhunters sampled fish from charterboat trips and lowest when captains reported tags (Fig. 2). Model coefficients indicated that the chance of recovering tags by creel clerks in non-chartered trips was about double the chance of CWT being reported by captains, by headhunters from non-chartered trips about three

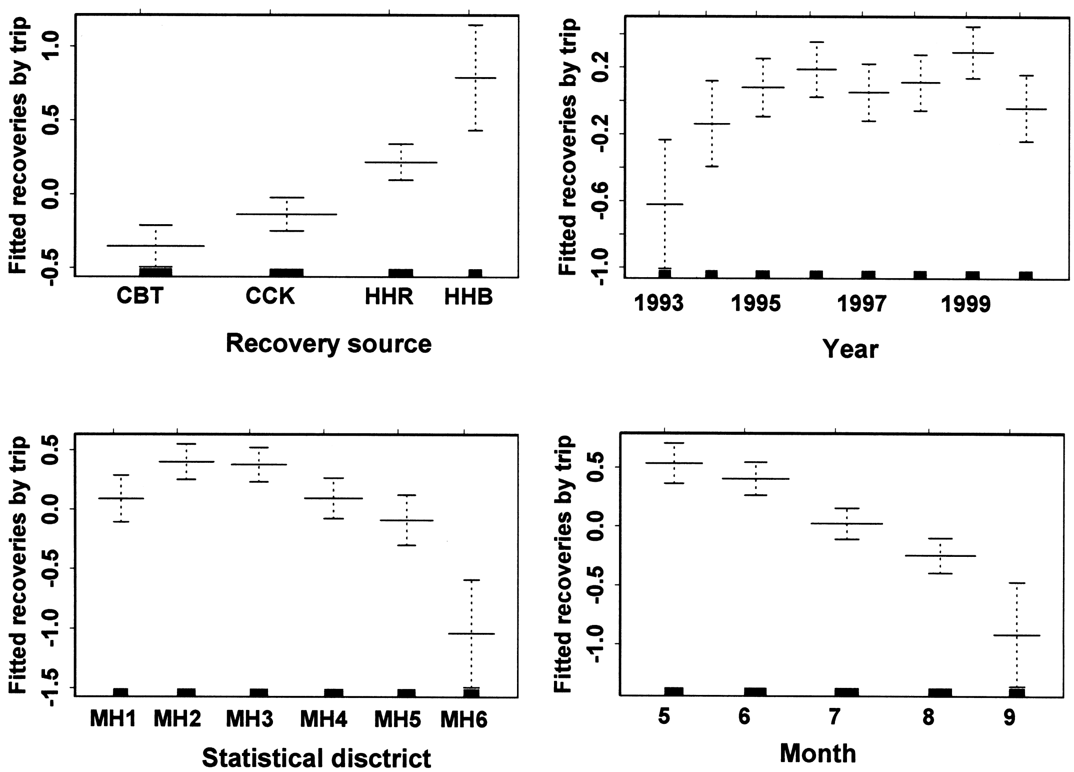

FIG. 2. Fitted effects from main effects binomial GLM, where coded wire tag recoveries from lake trout by trip are modeled as a function of (shown in clockwise direction) source of recovery (CBT = charter reported by captains, CCK = non-charter sampled by clerk, HHB = charter sampled by headhunter, and HHR = non-charter sampled by headhunter), year, month of recovery, and statistical district. The x-axes are for each predictor with corresponding factor levels, and filled boxes represent the relative amount of data used by level. The y-axes are standardized so that 0 represents the mean recoveries by trip in the logit link scale. Brackets indicate 95% confidence intervals.

times larger, and by headhunters from chartered trips about nine times larger (Table 4). The largest variation in recoveries by trip was among months, but they also varied significantly by statistical district and year fish were recovered (probability of Chi < 0.0001) (Table 4). Levels increased from 1993 to 1994 and were fairly similar in subsequent years, were highest in statistical districts MH-2 and MH-3, and decreased steadily from May to September (Fig. 2). The main effects GLM explained over 50% of the variation in the data; recovery sources accounted for 20% of the total variation explained, while months, areas, and years accounted for 39%, 28%, and 13% of the variation, respectively (Table 4). First order interactions between the source of recovery and the month, year, or statistical district were not significant (probability of Chi = 0.12), indicating that efficiency by each source of recovery remained relatively similar in time and space. Hence, the analysis does not appear to be influenced by differences in individual performance of creel clerks, headhunters or charterboat captains. The logit link resulted in smaller deviance than the complementary log-log and the probit link functions (1960.6, 1961.6, and 1982.5 respectively), and was used for all models. Inspection of model residuals showed neither outliers nor particular trends that might suggest lack of fit. The estimate of the dispersion parameter of the binomial GLM was close to 1, indicating no over-dispersion in the model.

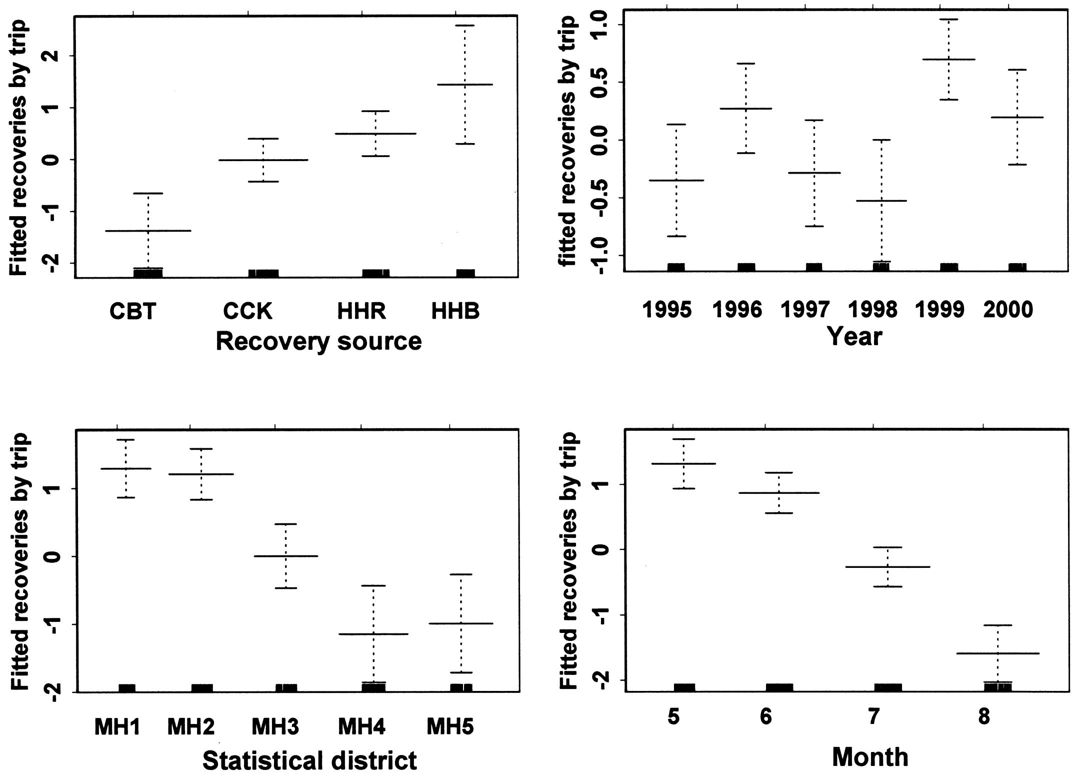

FIG. 3. Fitted effects from a GLM of coded wire tag recoveries by trip from lake trout released in MH-1 as a function of (shown in clockwise direction): recovery source, year, month, and statistical district of recovery. Other descriptions are as in Figure 2.

Distribution of CWT Fish Recoveries Relative to Release Area

Recoveries by trip of fish released in MH-1 were similar in the release area to those in neighboring district MH-2 to the south, and significantly higher than in more distant statistical districts (Fig. 3). Levels decreased from May to August (Fig. 3). Nevertheless, first order interaction between area and month was significant (probability of Chi = 0.005). While levels decreased towards the south during May and June, the latitudinal gradient disappeared toward the end of the season (Fig. 4). Because of the seasonal patterns in recoveries by trip, we identified the month of highest recovery levels to ran a month specific GLM. We selected May. As in the model for all months, coefficients in May were similar in MH-1 and MH-2 and higher than in other areas to the south (Table 5).

Recoveries by trip of fish released in MH-2 were similar in the release area to those in neighboring MH-3 to the south, and significantly higher than in MH-1, MH-4 and MH-5 (which were similar to each other) (Fig. 5). Overall, levels decreased from May to August (similar to the pattern shown in Fig. 3). The month-area interaction was significant (probability of Chi = 0.009). To generate estimates for the movement matrix we selected May, and the May coefficient for MH-2 was similar to MH-1 to the north (Table 5), instead of being similar the MH-3 coefficient to the south.

Recoveries by trip of fish released in MH-3 were similar in the release area to those in neighboring area MH-2 to the north, and significantly higher than in other areas (Fig. 5). Levels were lowest in MH-1 (Fig. 5), and decreased from May to August (similar to the pattern shown in Fig. 3). The interaction between month and area was significant (probability of Chi = 0.03). Further, there was a progression in highest fitted levels from MH-2 to MH-3 from May to June, which suggests that fish moved between areas during those months. Thus, we selected both months for generating indices for

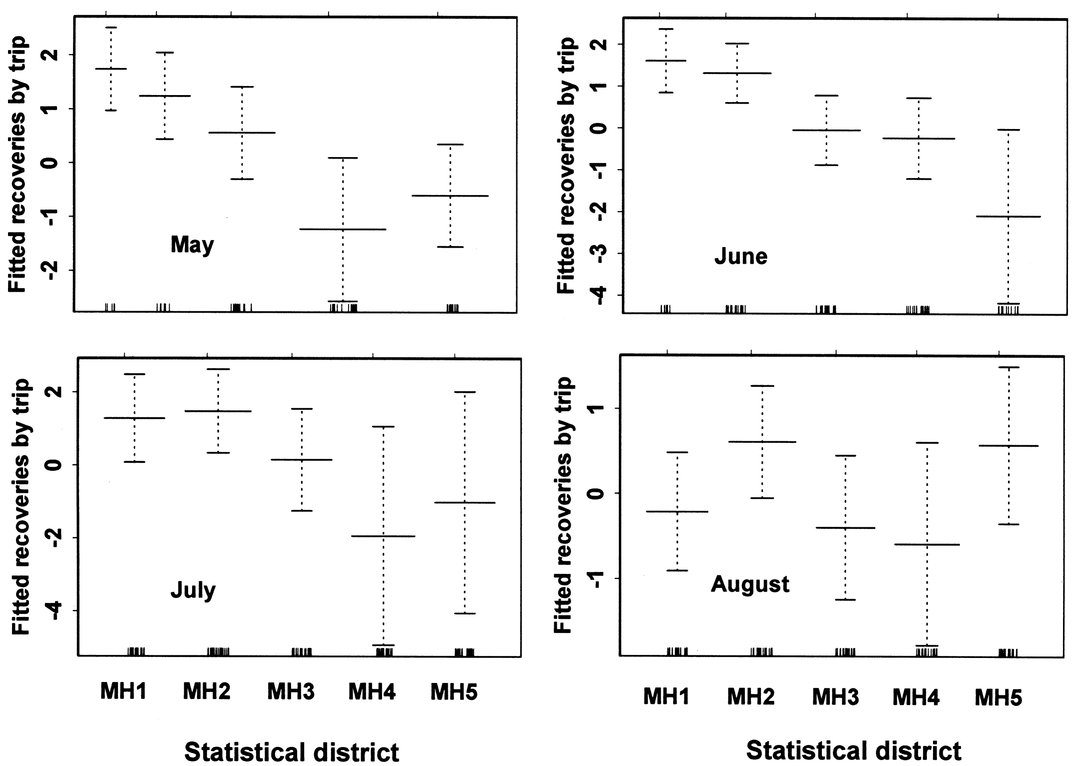

FIG. 4. Fitted area effects from GLMs of coded wire tag recoveries by fishing trip from lake trout released in MH-1 by month (May to August from 1995 to 2000). Models also included year, source of recovery, and recovery area as predictors. Other descriptions are as in Figure 2.

the movement matrix. In May, coefficients in the release area MH-3 and in MH-4 (to the south) were not significantly different and were higher than in MH-2 to the north (Table 5). In June, coefficients were similar in MH-3 and MH-2 and higher than in MH-4 (Table 5).

Recoveries by trip of fish released in MH-4 were similar in the release area to those in neighboring

TABLE 5. GLM area coefficients for lake trout CWT recoveries by trip relative to area of release for months when recovery levels were highest (May, June, or both). Models also include year and source of recovery as predictor (coefficients not shown). Area coefficients were estimated using a treatment contrast matrix with the release area as reference level (in bold). '=' no significant difference with the reference area.

	Release Area									
Recovery	MH-1		MH-2		MH-3		MH-3		MH-4	
Month	May		May		May		June		June	
Area	coef	t-value	coef	t-value	coef	t-value	coef	t-value	coef	t-value
MH-1	**–2.95**	**–14.107**	–0.02	–0.063 =	–1.12	–2.085	–2.18	–3.832	–2.24	–2.120
MH-2	–0.61	–1.820 =	**–3.27**	**–14.38**	–0.73	2.149	–0.25	–1.320 =	–1.90	–2.376
MH-3	–1.49	–3.247	–1.01	–2.287	**–3.91**	**–14.506**	**–3.45**	**–31.212**	–1.34	–2.134
MH-4	–3.25	–3.205	–1.54	–2.808	–0.21	–0.585 =	–0.64	–3.156	**–4.40**	**–11.609**
MH-5	–2.92	–3.983	–2.59	–3.516	–1.41	–2.726	–2.35	–4.654	–0.41	–0.694 =
MH-6	–	–	–	–	–	–	–	–	–2.46	–2.334

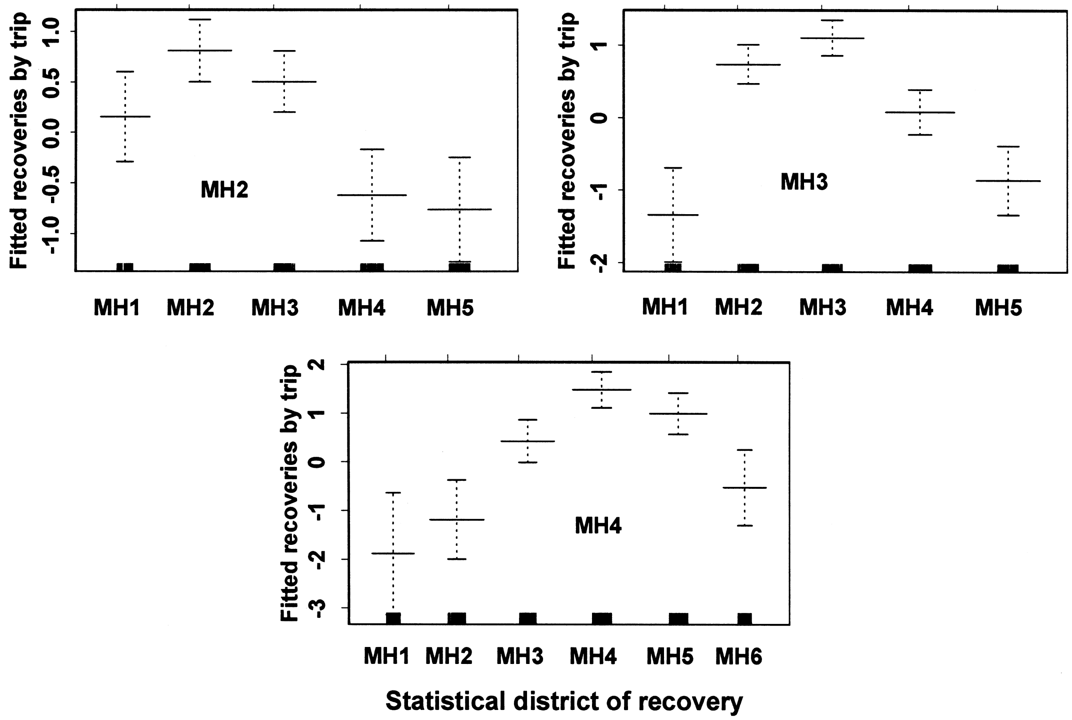

FIG. 5. Fitted area effects from GLMs of coded wire tag recoveries by trip from lake trout released in statistical districts MH-2, MH-3 and MH-4. Models also included source of recovery, year and month as predictors. Other descriptions are as in Figure 2.

MH-5 to the southeast, and significantly higher than in other areas, and were lowest in MH-1 and MH-2 (Fig. 5). Levels were high and similar during May and June, and decreased to lower and similar levels in July and August. The month-area interaction was significant (probability of Chi = 0.04). To generate estimates for the movement matrix we selected June. As in model for all months, June coefficients were

TABLE 6. Percentage of CWT lake trout released in statistical districts MH-1 to MH-4 and recovered in MH-1 to MH-6 from recreational fisheries 1993–2000, based on: i) "raw" CWT recoveries, ii) CWT data adjusted by number of trips, and iii) standardized GLM recoveries for May or June (same values for areas with coefficients not significantly different in Table 5).

		Recovery Area						
Release Area		MH-1	MH-2	MH-3	MH-4	MH-5	MH-6	Total
MH-1	Raw data	49	34	11.2	3.4	2.4	0.4	488
	Adjusted	46	34.9	10	3.4	4.4	0.9	
	GLM May	43.2	43.2	9.6	2.1	1.9	0	
MH-2	Raw data	17.8	36.2	29.8	8.2	6	2	583
	Adjusted	15.2	34	24.4	11.1	11.3	4	
	GLM May	38.1	38.1	13.9	7.9	2.0	0	
MH-3	Raw data	5.1	32.3	37	16.3	8.2	1.1	1,125
	Adjusted	5.2	31.2	27.8	19.8	15.2	0.8	
	GLM May	7.1	43.8	22.1	22.1	4.9	0	
	GLM June	4.1	36.2	36.2	19.6	3.9	0	
MH-4	Raw data	1.3	3.3	18.1	45	25.2	6.1	360
	Adjusted	1.2	3.8	9.9	43.1	32.7	9.3	
	GLM June	4.8	6.1	9.1	38.2	38.2	3.6	

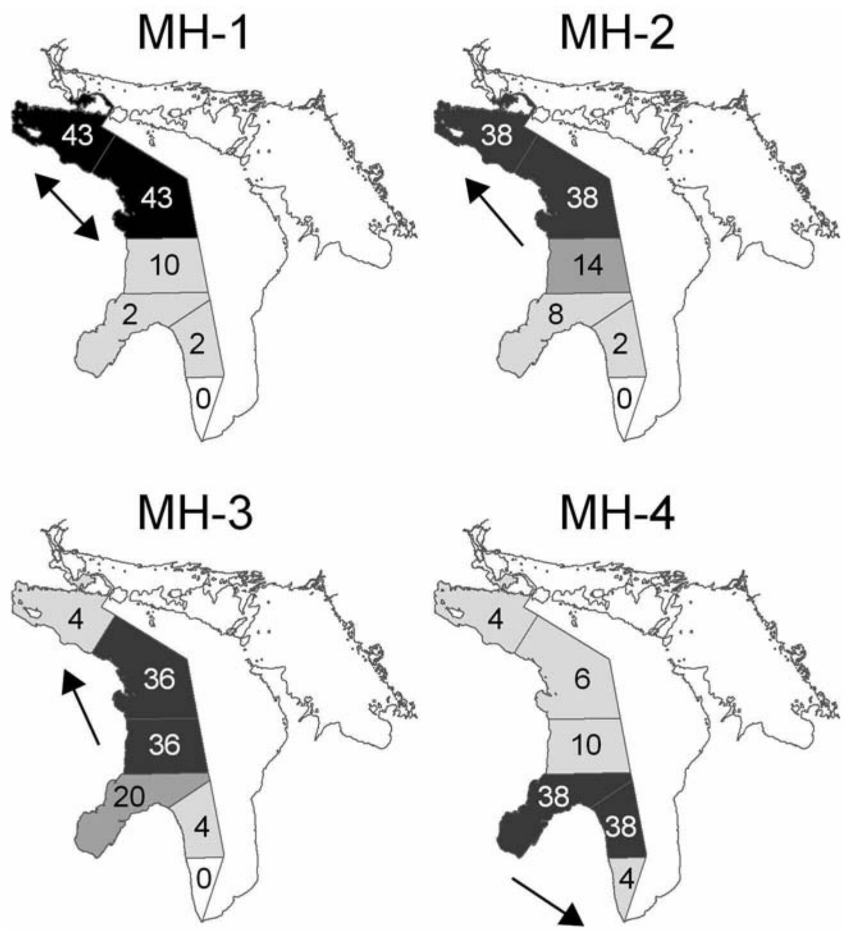

FIG. 6. Overall distribution of lake trout coded wire tag recoveries, expressed as standardized percentages predicted from GLMs estimates that account for the source of recovery. Data for the analysis are from the 1993 to 2000 recreational fisheries released in statistical districts MH-1 to MH-4 and the month of highest recovery rates (May or June as indicated in Table 5). The arrows indicate the inferred direction of movement.

similar in MH-4 and MH-5, and significantly different than those for other areas (Table 5).

Movement Matrix and Interpretation of Movement

The standardized percentages of CWT lake trout recovered in the areas where they had been released based on GLM predictions ranged from 22 to 43% (Table 6), and were similar in neighboring areas either to the north or the south. Percentages calculated based on the raw data or adjusted for fishing effort showed different patterns (Table 6).

For fish released in MH-1, based on standardized recoveries, 43% of CWT lake tout were found in the release area and in MH-2 to the south (Table 6), suggesting that fish moved in both directions (Fig. 6) since the site in MH-1 at which most fish were released was near the boundary between these two areas (Fig. 1). Percentages of non-standardized CWT remaining in MH-1 were slightly higher and steadily decreased towards the south indicating that fewer fish moved south (Fig. 6). For fish released in MH-2, based on standardized recoveries 38% of the tagged fish were found in the release area and in neighboring MH-1 (Table 6) indicating a net northward movement (Fig. 6). Percentages of non-standardized recoveries were highest in MH-2 and second highest in MH-3 suggesting that fish moved mostly to the south (Table 6). For fish released in MH-3, based on standardized recoveries in May 44% of the tagged fish were found north in MH-2 and only 22% were found in the release area indicating movement toward the north. For June 36% of the tagged fish were found in the release area and in MH-2 indicating net movement northward but also movement from MH-3 to MH-2. Thus, from the patterns observed on CWT lake trout distribution of recoveries of fish released in MH-3 we also can infer that fish moved from MH-2 to MH-3 during May and June. Non-standardized percentages of fish released in MH-3 were higher in MH-2 than in the release area and we can also infer northward movement. For fish released in MH-4, standardized proportions of recoveries (38%) were similar in MH-4 and MH-5 indicating that fish moved to the south. Further, given the location of the release site (Fig. 1), and because lake trout only occupy the east area of MH-4 (excludes Saginaw Bay), we can infer that net movement was to the southeast (Fig. 6). The percentages of recovery from non-standardized recoveries were highest in MH-4 suggesting less movement out of the release area.

DISCUSSION

Results from our GLM analysis for CWT lake trout data provide coefficients to standardize CWT recovery data from several recovery sources in the Lake Huron recreational fisheries, and to characterize CWT fish distribution to study movement. Our results improve current understanding of lake trout movement from release to recovery areas, and provide detailed information on fish spatial distributions as well as information on temporal movements.

Results from our analysis suggest that higher proportions of lake trout move out of the released area than previously shown, thus movement is less localized. We found that less than half of the CWT lake trout remained within the statistical areas of release in western Lake Huron, and that there was significant movement along the coast to other districts, and also seasonal displacement among areas. We speculate that displacement also took place away from statistical areas in US waters into Canadian management units. The differences in apparent movement of lake trout between our results and previous studies emphasize the need for standardizing recoveries by recovery sources and effort.

The results of tagged fish distribution based on standardized CWT recoveries are not only indicative of lake trout movement but also provide information on lake trout population dynamics. Fish released in each area were found in all areas, generally in percentages that decreased with distance. If proportions of CWT recoveries by area are indicative of the extent of movement, our results indicate that movements from fish released in each area were fairly similar, except for fish released in MH-1 that were less likely to move (43% recovered in release area vs. average of 36% for the other areas). Some of the movement patterns, nevertheless, may be biased by area-specific natural and fishing (commercial) mortality occurring over several years of early life before lake trout recruit to the recreational fishery. Highest natural mortalities caused by sea lamprey *Petromyzon marinus* are reported for northern areas (Sitar *et al*. 1999, Woldt 2003, Johnson *et al.* 2004), in particular for statistical area MH-1. Fishing mortality imposed by the recreational fishery should be high in areas MH-1 to MH-4 relative to MH5 and MH6 based on the number of effective trips for lake trout calculated in this study, and fishing mortality by the commercial fishery should be highest in MH-1, where lake trout are commercially harvested and also caught as bycatch of the whitefish and bloater chub fisheries (Woldt 2003). During the years of the study, instantaneous mortality in MH-1 induced by sea lampreys averaged around 0.30 and commercial fishing mortality was 0.19 (Woldt 2003, Johnson *et al*. 2004). Thus, fish that migrate out of MH-1 should experience higher survival rates and recruit to the recreational fisheries better than those that do not emigrate, and could bias our movement indices. Since MH-1 is the area where highest mortality occurs, we can expect that if fish start migrating at young ages, the population in that area may be more sedentary than reflected by the data.

Our results also show that recoveries by trip of CWT fish recovered in neighboring areas were not significantly different than those in the release area, with distribution of standardized percentages recovered by area suggesting displacement of tagged fish to the north, south, and southeast. We are cautious in our interpretation about directional movement because of tagged fish losses to mortalities which vary by management area, and also since most release sites were very close to the district boundaries (less than 25 km from MH-1, MH-3 and MH-4, Fig.1); simple dispersion should result in similar distribution in the release and the neighboring areas. Nevertheless, location of the release site could not account for CWT recovery distribution and the apparent directional movement of fish released in MH-2 towards the north, since the stocking locations are at least 50 km from the MH-1 boundary. Stocking location could contribute to apparent movement of fish released in MH-4 toward the south and east, since the stocking site was on the south-east corner of MH-4 [Pt. Aux Barques is very near the boundary line separating MH-4 from MH-5 and most fishing effort is near or SE of this stocking site]. Martin and Olver (1980) and Schmalz *et al.* (2002) proposed that lake trout are nomadic and move in response to factors such as spawning, food, and environmental conditions, but that some movement is random. We refrain from discussing factors that could influence directional movement in our study since we do not know when movement occurred from the release areas.

The matrix representing CWT lake trout distribution by statistical area of release, and used to infer movement in this study, was different than that obtained by Madenjian *et al*. (2003) (Table 2). The main differences are that based on our lower proportions of fish released and recovered in MH-1 (43% vs. Madenjian et al. 2003 estimate of 64%), movement of fish released in the area is interpreted to be less localized, while the opposite is true for MH-4 (38 vs. 26%). Recoveries in Madenjian *et al.* (2003) included younger fish from gillnet surveys and commercial fisheries than recoveries available from recreational fisheries in our study. Thus, the discrepancy in proportions reported in MH-1 can be influenced by older fish in our data that moved larger distances and suffered mortality from all sources in MH-1 before recruiting to the recreational fishery. The discrepancy in proportions in MH-4 can be attributed to the number of fish that move to Canadian waters, which was estimated at about 18% (Madenjian *et al.* 2003), and was not included in our analysis. Discrepancies can also be due to the lack of standardization of recoveries among recovery sources in Madenjian *et al.* (2003), and to the inclusion of data from several months. Our matrix compares to a lesser degree to that used for assessment (Woldt 2003) (Table 2). In that matrix, 97 and 86% of the releases in refuges (Drummond Island located in MH-1 and Six Fathom Bank in MH-2) remained within the management unit containing the refuges. In our matrix, more than half of the fish released in districts where refuges are present were found in other areas, and although we did not perform analysis for recoveries of releases in refuges and inshore locations separately, we know that 80% of the CWT recoveries that we used in our analysis were from releases in refuge areas. Our results suggest that movement out of MH-1 and MH-2 is underestimated, and fish stocks in those areas are overestimated. It is possible that given the data sources our analysis is biased against fish that remained in the refuges, while Woldt (2003) is biased in favor of fish that remained within refuges, especially since much survey effort in MH-1 and MH-3 was focused on the refuges.

Results from this study showed that CWT recoveries by trip decreased from May to September, with differences in the patterns among areas, and raises the general issue of whether data from all months should be combined to implement movement matrices. The temporal decline can result from fish mortality, latitudinal migrations, movements in and out of refuge areas, movement to greater depths that are less accessible to recreational fishing, and from anglers shifting target species from lake trout (May–June) to chinook salmon (July–September). We estimated that this change in target species represents a ten-fold drop in the average catch rate in the non-charter fishery during the years of the study.

Results suggest that fish not only move from release areas to other areas but also that also that they move among statistical districts during the fishing season, which can have consequences for stock assessment models. Lake trout stock assessment models assume that movement among areas occurs only during the first year after stocking (Woldt 2003). In this study, we found fish movements during the fishing season between statistical areas MH-2 and MH-3, and we suspect they also occur elsewhere but could not be identified due to small sample sizes available. To incorporate seasonal movements occurring among areas, the assessment model, rather than adjusting the numbers recruited to each management area every year for mortality in the same area, would need to consider that a fraction of the population in each area is exposed to fishing and natural mortality in other areas. Further, our results suggest that the assumption (for assessment) that movement occurs soon after stocking before spatially-varying mortality occurs needs to reconsidered, and that a revised stock assessment model should include age-dependent movement and temporally- and spatially-explicit mortality.

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REFERENCES

Becker, R.A., Chambers, J.M., and Wilks, A.R. 1988. *The new S language. A programming environment for data analysis and graphics.* Pacific Grove, California: Wadsworth & Brooks/Cole Advanced Books & Software.

Buettner, H.J. 1961. Recoveries of tagged, hatchery reared lake trout from Lake Superior. *Trans. Am. Fish. Soc.* 90:404–412.

Coble, D.W., Bruesewitz, R.E., Fratt, T.W., and Scheirer, J.W. 1990. Lake trout, sea lampreys, and overfishing in the upper Great Lakes: a review and reanalysis. *Trans. Am. Fish. Soc.* 119:985–995.

Ebener, M.P. (ed). 1998. *A lake trout rehabilitation guide for Lake Huron.* Great Lakes Fishery Commission, Ann Arbor, Michigan.

Eschmeyer, P.H. 1957. *The lake trout* (Salvelinus namaycush) U.S. Dept. Interior Fishery Wildlife Service, Fishery Leaflet No 441.

_____, Daly, R., and Erkkila, L.F. 1953. The movement of tagged lake trout in Lake Superior, 1950–1952. *Trans. Am. Fish. Soc.* 82 (1952):68–77.

Eshenroder, R.L., Payne, N.R., Johnson, J.E., Bowen II, C.A., and Ebener, M.P. 1995. Lake trout rehabilitation in Lake Huron. *J. Great Lakes Res.* 21 (Supplement 1):108–127.

Goñi, R., Alvarez, F., and Adlerstein, S.A. 1999. Application of generalized linear modelling to catch rate analysis of western Mediterranean fisheries: the Castellón fleet as a case study. *Fisheries Research* 42:291–302.

Gulland, J.A. 1969. *Manual of methods for fish stock assessment, part 1. Fish population analysis.* FAO (Fish and Agriculture Organization of the United Nations) Manuals in Fisheries Science 4, FRS/M4.

Hansen, M.J., Peck, J.W., Schorfhaar, R.G., Selgeby, J.H., Schreiner, D.R., Schram, S.T., Swanson, B.L., MacCallum, W.R., Burnham-Curtis, M.K., Curtis, G.L., Heinrich, J.W., and Young, R.J. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration 1959–1993. *J. Great Lakes Res.* 21 (Suppl. 1):152–175.

Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Can. J. Fish. Aquat. Sci.* 47:635–643.

_____, and Walters, C. 1992. *Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty.* London: Chapman & Hall.

Hile, R. 1949. Trends in the lake trout fishery of Lake Huron through 1946. *Trans. Am. Fish. Soc.* 76(1946): 121–147.

Johnson, J.E., and VanAmberg, J.P. 1995. Evidence of natural reproduction of lake trout in western Lake Huron. *J. Great Lakes Res.* 21 (Supplement 1): 253–259.

_____, Wright, G.M., Reid, D.M., Bowen II, C.A., and Payne, N.R. 1995. Status of the cold-water fish community in 1992. In *The State of Lake Huron in 1992,* M.P. Ebener, ed., pp. 21–17. Great Lakes Fishery Commission, Special Publication 95-2, Ann Arbor, Michigan.

_____, He, J.X., Woldt, A.P., Ebener, M.P., and Mohr, L.C. 2004. Lessons in rehabilitation stocking and management of lake trout in Lake Huron. *American Fisheries Society Symposium,* 44:161–175.

Lawrie A.H. 1970. The Sea lamprey in the Great Lakes. *Trans. Am. Fish. Soc.* 99:66–775.

Madenjian, C., DeSorcie, T., McClain, J., Woldt, A., Ebener, M., and Johnson, J. 2003. *Lake Trout Rehabilitation in Lake Huron—2002.* Progress Report on Coded-Wire Tag returns. Ann Arbor, Michigan: Great Lakes Fishery Commission.

Martin, N.V., and Olver, C.H. 1980. The lake charr, *Salvelinus namaycush* In *Charrs: salmonids fishes of the genus Salvelinus,* E.K. Balon, ed., pp. 205–277. The Hague, The Netherlands: Dr. W. Junk Publisher.

Maunder, M., and Punt, A. 2004. Standardizing catch and effort data: a review of recent approaches, *Fisheries Research* 70:141–159.

McCullagh, P., and Nelder, J.A. 1989. *Generalized Linear Models.* London: Chapman & Hall.

Pycha, R.L., Dryer, W.R., and King, G.R. 1965. Movements of hatchery-reared lake trout in Lake Superior. *J. Fish. Res. Board Can.* 24:999–1024.

Rahrer, J.F. 1968. Movements of adult lake trout in Lake Superior. *Trans. Am. Fish. Soc.* 97:481–484.

Rybicki, R.W. 1990. *Growth, survival, and straying of the three lake trout strains stocked in the refuge of northern Lake Michigan.* Michigan Department of Natural Resources Fisheries Research Report 1977, Ann Arbor, Michigan

_____, and Keller, M. 1978. *The lake trout resources in Michigan waters of Lake Michigan, 1970–1976.* Michigan Department of Natural Resources Fisheries Report No. 1836, East Lansing, Michigan.

Schmalz, P.J., Hansen, M.J., Holey, M.E., McKee, P.C., and Toneys, M. 2002. Lake trout movements in Northwestern Lake Michigan. *North American Journal of Fisheries Management* 22:737–749.

Smith, O.H., and Van Oosten, J. 1939. Tagging experiments with lake trout, whitefish and other species from Lake Michigan. *Trans. Am. Fish. Soc.* 69:63–84.

Sitar, P.S., Bence, J.R., Johnson, J.J., Ebener, M. and Taylor, W. 1999. Lake trout mortality and abundance in Southern Lake Huron. *North American Journal of Fisheries Management* 19:881–900.

Swanson, B.L. 1973. *Lake trout homing, migration, and mortality studies, Lake Superior.* Wisconsin Department of Natural Resources, Fish Management Report 65, Madison, Wisconsin.

Venables, W.N., and Ripley, B.D. 2000. *Modern applied statistics with S-Plus.* 3rd ed. New York: Springer-Verlag, Inc.

Woldt, A.P. 2003. Status of Lake Trout Populations in MH-1 and MH-2. In *Summary Status of Lake Trout and Lake Whitefish Populations in the 1836 Treaty-Ceded Waters of Lakes Superior, Huron and Michigan in 2001, with recommended yield and effort levels for 2002,* J.R. Bence, M.P. Ebener, S.P. Sitar, and A.P. Woldt, eds. Technical Fisheries Committee, 1836 Treaty-Ceded Waters of Lakes Superior, Huron and Michigan.

_____, Reid, D.M., and Johnson, J.E. 2005. The Open-Water Predator Community. In *The State of Lake Huron in 1999*, M.P. Ebener, ed., pp. 47–68. Great Lakes Fishery Commission Spec. Pub. 05-02.

_____, Sitar, S.P., Bence, J.R., and Ebener, M.P. (eds.). 2006. *Summary Status of Lake Trout and Lake Whitefish Populations in the 1836 Treaty-Ceded Waters of Lakes Superior, Huron and Michigan in 2004, with recommended yield and effort levels for 2005.* Technical Fisheries Committee, 1836 Treaty-Ceded Waters of Lakes Superior, Huron and Michigan.

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